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Asymmetrical insect invasions between three world regions

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Abstract

The geographical exchange of non-native species can be highly asymmetrical, with some world regions donating or receiving more species than others. Several hypotheses have been proposed to explain such asymmetries, including differences in propagule pressure, source species (invader) pools, environmental features in recipient regions, or biological traits of invaders. We quantified spatiotemporal patterns in the exchange of non-native insects between Europe, North America, and Australasia, and then tested possible explanations for these patterns based on regional trade (import values) and model estimates of invader pool sizes. Europe was the dominant donor of non-native insect species between the three regions, with

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most of this asymmetry arising prior to 1950. This could not be explained by differences in import values (1827–2014), nor were there substantial differences in the sizes of modelled invader pools. Based on additional evidence from literature, we propose that patterns of historical plant introductions may explain these asymmetries, but this possibility requires further study.

Keywords
International trade, non-native insects, plants, propagule pressure, species pools

Introduction

Non-native insects have been implicated in displacing native species, altering the composition of ecological communities, damaging economically important trees and food crops, vectoring diseases, and more (Kenis et al. 2009; Bradshaw et al. 2016). An intriguing aspect of insect invasions is that some regions appear to have donated disproportionately more non-native insects during biotic exchange than others. For example, considerably more phytophagous forest insects have invaded North America from Europe than the reverse (Niemelä and Mattson 1996), and Europe has contributed a large fraction of New Zealand's non-native insect fauna (Edney-Browne et al. 2018). Consequently, the question of why such asymmetries may occur has fascinated ecologists for decades, with several mutually compatible hypotheses offered: (1) differences in the magnitude of invasion vectors, such as international trade, may lead to differences in the arrival and establishment rates of non-native species; (2) differences in the size of potential invader pools may drive differences in the numbers of species being donated to other regions; (3) environmental differences (e.g., climate and availability of host plants) in recipient regions may promote or inhibit invasion; and (4) biological traits of insects native to some regions may make them better at invading or competing than insects native to other regions (Vermeij 1991, 1996; Niemelä and Mattson 1996; Visser et al. 2016).

The latter two hypotheses are often tested on a single insect order or guild and at smaller spatial scales (e.g., Rigot et al. 2014; Guyot et al. 2015; Rassati et al. 2016), but less commonly on multiple insect orders and multiple geographical regions. Testing them requires regional knowledge of the nature of recipient environments and their ecological communities, and of the biological traits of the invaders, information that is often available only for certain regions or certain insect groups/guilds. The former two hypotheses are more approachable, given the availability of datasets on international trade, regional insect richness, and modelling approaches that can estimate invader pool sizes.

Our research goals were firstly to test for the existence of asymmetries in the cumulative numbers of insect invaders, across all taxa, exchanged between three world regions of interest: North America, Europe, and Australasia (limited to Australia and New Zealand). These regions were chosen due to their histories of anthropogenic interactions and exchange of species, existing literature suggesting asymmetrical exchange of insects between them (see above), and the availability of data. Secondly, if clear

asymmetries were found, we aimed to determine if they could be explained by differences in propagule pressure (using the value of international trade as a proxy) or by differences in estimates of invader pool sizes. We did not statistically test hypotheses (3) and (4), above, but considered them as possible explanations for asymmetries that could not be explained by hypotheses (1) and (2).

Methods

Datasets and world regions

Insect establishment data were based on the International Non-native Insect Establishment database (Turner et al. 2021), supplemented by several other online datasets (Seebens et al. 2017; Nahrung and Carnegie 2020; Liebhold et al. 2021; GBIF.org 2022; Mally et al. 2022). We used an automated taxonomic cleaning script (Blake and Turner 2021) using the GBIF (GBIF.org 2022) API to standardize species names (merge synonyms and correct misspellings). The resulting dataset contained dated records of non-native insect discoveries, the species identity (order, family, genus, and species), the region/nation in which the species was discovered, the native biogeographic range of the species, and other data such as whether the introduction was deliberate, if the species was found only indoors (e.g., greenhouses), and if the species is herbivorous.

Our choices of world regions and their spatial extents were constrained by the available data. We used a subset of the establishment database that allowed us to compare the reciprocal flows of insects between donor and recipient regions. The only regions that could be compared in this way were North America (NA), Europe (EU), and Australia and New Zealand combined into an Australasian region (AU). Due to spatial gaps in these data, there were minor mismatches in the spatial extents of these regions depending on context. For example, as a donor region, Australasia included Papua New Guinea, but as a recipient region, it only included Australia and New Zealand because we did not have non-native insect discovery records for Papua New Guinea. In this case, correcting for this mismatch would require estimating the number of insects from North America and Europe that have established into Papua New Guinea, and excluding species that also established into Australia or New Zealand. Since the spatial mismatches were relatively minor, and such corrections would themselves be prone to error, we opted not to attempt corrections.

For all analyses, we excluded discovery records where: (1) species had native ranges spanning multiple biogeographic regions (e.g., Holarctic or cosmopolitan species); (2) the native ranges and establishment regions were the same (indicating species that spread within these regions); (3) the establishment was limited to "indoors" (e.g., greenhouses); or (4) the establishment was a result of intentional introduction. This left us with a dataset of 2,324 non-native insect discovery records across the six pairwise flows between North America, Europe, and Australasia, with the dated records spanning 1617–2021.

Regional import value data were obtained from the TradeHist database (Fouquin and Hugot 2016), modified with modern ISO-3 country codes. The TradeHist database describes the annual value of trade goods from 1827–2014 in British pounds sterling (not corrected for inflation) flowing from origin to destination countries. The database does not include details on trade volume/frequency or commodity type. We corrected all trade values for inflation relative to 2020 based on the annual percent change of the UK retail prices index (Office for National Statistics 2021). We grouped the origin and destination countries into the same regions as above (North America, Europe, and Australasia), with some minor unavoidable differences where national borders did not follow biogeographic boundaries. From these groupings of countries, we created a subset of the TradeHist database representing the six pairwise flows between North America, Europe, and Australasia by summing annual trade value across all countries within each region. Records of trade between countries within each of the resulting biogeographic regions were dropped.

Testing for asymmetries and temporal variation in establishment rates

To test for invasional asymmetries, we tallied the number of first discoveries of non-native insects for each of the six pairwise flows between North America, Europe, and Australasia. We further split these cumulative counts by insect order and (separately) by herbivory (herbivores vs non-herbivores). We used G-tests (log-likelihood ratio goodness-of-fit tests) to compare these counts between each donor/recipient pair, separately for each order and herbivory category (e.g., one test for the counts of Coleoptera exchanged in both directions between Europe and North America, another for Hemiptera, etc.), with the null hypothesis being equal numbers of insects exchanged in each direction. We adjusted the *P*-values for multiple comparisons across orders and herbivory categories using the Holm-Bonferroni procedure. To visualize temporal variation in the establishment rates of insects over each flow, we plotted cumulative discoveries versus cumulative import values following Levine and D'Antonio (2003).

Testing for the effects of differential trade and invader pool sizes

To determine if asymmetries in non-native insect establishments between regions could be explained by unequal trade or invader pools, we adapted Poisson process models from Costello et al. (2007) and Morimoto et al. (2019) in which the number of annually established insects flowing from donor to recipient regions were proportional to annual import values and model-fit invader pool sizes. Because the Poisson-process models required dated annual discovery and import values for each observation, this limited our establishment records to the date range of the TradeHist database. This left us with 1,872 dated establishment records (~80% of the establishment dataset) with corresponding import values from 1827–2014.

Our models estimated the lag between establishments and discoveries, predicting the annual establishments necessary to fit to observed discoveries given the lag estimates. This was done to address concerns over records of first discovery being poor

proxies for the actual timing of establishments given the extended lag frequently occurring between establishment and discovery (Costello and Solow 2003). As discovery probability depends in large part on discovery effort, this allows our models to (indirectly) account for overall differences in discovery effort between flows.

To account for the possibility of "saturation" (depletion of invader pools) that might gradually reduce establishment rates, we used AIC-based model selection to choose between models which included or omitted a rate-limiting component based on the observed number of cumulative discoveries compared to a predicted maximum. All models contained an 'annual establishment rate' parameter (r) representing the number of non-native insects per billion pounds sterling of imports prior to any depletion of invader pools. If differences in import values fully explained asymmetries in non-native insect establishments, we would expect no significant differences between reciprocal flows in the value of r.

We omitted an intercept term in our models, forcing them to account for all establishments as a function of imports. We modelled the gradual depletion of invader pools as a non-linear rate-limiting factor based on the idea that early invaders are more likely the best or most numerous invaders, leading to a rapid initial decrease in the probability of establishment per unit of propagule pressure (Liebhold et al. 2017). These modifications were necessary to produce good fits to our data – initial attempts to use the same models as in Morimoto et al. (2019) resulted in nonsensical parameter estimations and poor fits in most cases. Our full model was:

$$\lambda_t = r v_t s_t$$

$$s_t = \left(1 - \frac{d_{c,t}}{d_{sat}}\right)^2 \qquad (1)$$

$$N_t \sim \text{Poisson}\left(\delta_t = \sum_{j=1827}^{t} \lambda_j p_t\right)$$

$$p_{j,t} = \pi\,(1 - \pi)^{t-j},$$

where:
λ_t is the predicted number of new non-native establishments in year t,
r is the number of species established per billion pounds sterling (prior to saturation),
v_t is the value of imports (2020 billion pounds sterling) in year t,
s_t is a rate-limiting factor of interval [0,1] which approaches 0 as the cumulative number of species discoveries approaches a predicted maximum,
$d_{c,t}$ is the (observed) cumulative species discovered by year t,
d_{sat} is the number of discoveries after which new establishments cease (saturate),
N_t is the actual number of non-native discoveries in year t,
δ_t is the predicted number of non-native discoveries in year t,
$p_{j,t}$ is the probability that a species which established in year j will be discovered in year t,
and π is the annual probability of discovery.

The cumulative sum of discoveries ($d_{c,t}$) was calculated by summing the number of annual discoveries from the first year of records (1827) to year t, inclusive. We used the sum of discoveries instead of establishments for modelling the saturation of species pools because discovery sums could be easily calculated from the original data. The main drawback to this technique was that it slightly complicated the interpretation of the saturation parameter (d_{sat}): rather than being a direct prediction of the invader pool size, it was the predicted number of cumulative discoveries at the time of full depletion of the invader pool.

We fit the models to observed annual discoveries (N_t) for each combination of donor and recipient region, minimizing the maximum likelihood as described by Morimoto et al. (2019):

$$L(r, d_{sat}, \pi) \propto \prod_{j=1827+\tau}^{t} \exp(-\delta_j)\, \delta_j^{N_j} \tag{2}$$

where τ = 20 as "preservation years" to prevent fitting the model to species that established prior to 1827 (the first year of discovery records in our database) but were discovered after 1827. Without these "preservation years", δ_t (the predicted number of discoveries in year t) may be underestimated near the start of the dataset because there will be a lack of prior years of predicted establishments from which to model the lagged discoveries (Morimoto et al. 2019). We also used a reduced model which omitted the depletion of invader pools from Eq. (1), effectively making s_t a constant with a value of 1. We then removed the associated parameter (d_{sat}) from Eq. (2). This "without saturation" model was otherwise identical to the full model.

For parameter estimation, we set lower and (in a few cases) upper bounds on each parameter using the Limited-memory Broyden–Fletcher–Goldfarb–Shanno algorithm (L-BFGS-B) method (Byrd et al. 1995). We bounded the rate of establishments (r) to ≥ 0.005 non-native species per billion pounds sterling of imports. This was done to prevent model optimization from testing ecologically nonsensical parameter estimates (negative or zero species introductions per billion pounds sterling of imports); 0.005 was chosen to be well below the initial slopes of the curves of cumulative non-native species versus cumulative import values. We bounded the annual probability of discovery (π) to between 0.0125 and 0.95 (corresponding to 1.05–80 years of discovery lag), which was chosen as an ecologically reasonable range based on discovery lag estimates from prior publications (Morimoto et al. 2019; MacLachlan et al. 2021). If the lag estimates were left unbounded, the models typically failed to converge. For the saturation term (d_{sat}), we set the lower bound to the cumulative numbers of observed, dated discoveries of non-native insects (since we know the invader pool must be at least this large). This lower bound varied for each of the six flows (1121 for EU to NA, 205 for NA to EU, 349 for EU to AU, 70 for AU to EU, 74 for NA to AU, and 53 for AU to NA). We did not impose an upper bound on the estimates of d_{sat}. We fit both the full and reduced models (the latter lacking the saturation term) to each flow and selected the one with the lowest Akaike information criterion (AIC) value.

To determine if asymmetries may be explained by differences in the size of invader pools, we compared 95% confidence intervals of the predicted numbers of non-native

insect discoveries after full depletion of the invader pool (d_{sat}) between region pairs resulting from our Poisson process models. This was only done when full models (including terms for finite invader pools) were selected for both directions between region pairs. Additionally, we compiled counts of described native insects in each of the three regions for qualitative comparisons to the magnitude of insect invasions across the six flows.

We used the *R* function *optim* for parameter estimation in the Poisson process models (R Core Team 2021). The confidence intervals were approximately calculated using the inverse of the Hessian matrix evaluated at the last iteration in the optimization process. For parameters with lower or upper bounds, we truncated the confidence intervals to the parameter estimation boundaries. All analyses were performed in R 4.1.0 (R Core Team 2021). Model predictions (cumulative annual establishments and discoveries) were included on the plots of cumulative discoveries versus cumulative trade.

Results

Europe has donated approximately six times more non-native insect species to North America and Australasia than it has received from these regions (Fig. 1).

Asymmetries in the reciprocal flows of non-native insects between Europe and North America and between Europe and Australasia were highly significant in total species, across the five largest insect orders, and among both herbivores and non-herbivores (all $p < 0.001$; Table 1). There were no significant asymmetries in the numbers of non-native insects exchanged between North America and Australasia (all $p > 0.05$; Table 1).

Plots of cumulative insect establishments versus cumulative import values over time show that the European asymmetry developed quickly and early (Fig. 2). In

Table 1. Counts of non-native insect species discovered for each of the six pairwise flows between North America (NA), Europe (EU), and Australasia (AU), by taxonomic order, herbivory, and sum totals. Col. = Coleoptera, Hem. = Hemiptera, Hym. = Hymenoptera, Lep. = Lepidoptera, Dip. = Diptera. The *G* statistic was computed to test the null hypothesis of no difference in the number of species exchanged in each direction between a given pair of world regions, separately for each column. We used the Holm-Bonferroni method to control for multiple comparisons across orders and herbivory.

Flow	Order						Herbivory		Total
	Col.	Hem.	Hym.	Lep.	Dip.	Other	Yes	No	
EU to NA	477	368	211	144	138	76	854	560	1414
NA to EU	40	72	54	20	29	15	160	70	230
G ($df=1$)	435	218	99.4	106	77.3	44.7	522	434	948
p ($\geq G$)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
EU to AU	137	96	67	31	55	57	226	217	443
AU to EU	34	10	14	7	4	8	41	36	77
G ($df=1$)	66.5	80.7	37.7	16.4	52.5	41.6	141	144	285
p ($\geq G$)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
NA to AU	20	26	13	8	10	11	57	31	88
AU to NA	18	22	15	4	6	7	48	24	72
G ($df=1$)	0.11	0.33	0.14	1.36	1.01	0.90	0.77	0.89	1.60
p ($\geq G$)	~ 1	~ 1	~ 1	~ 1	~ 1	~ 1	0.69	0.69	0.21

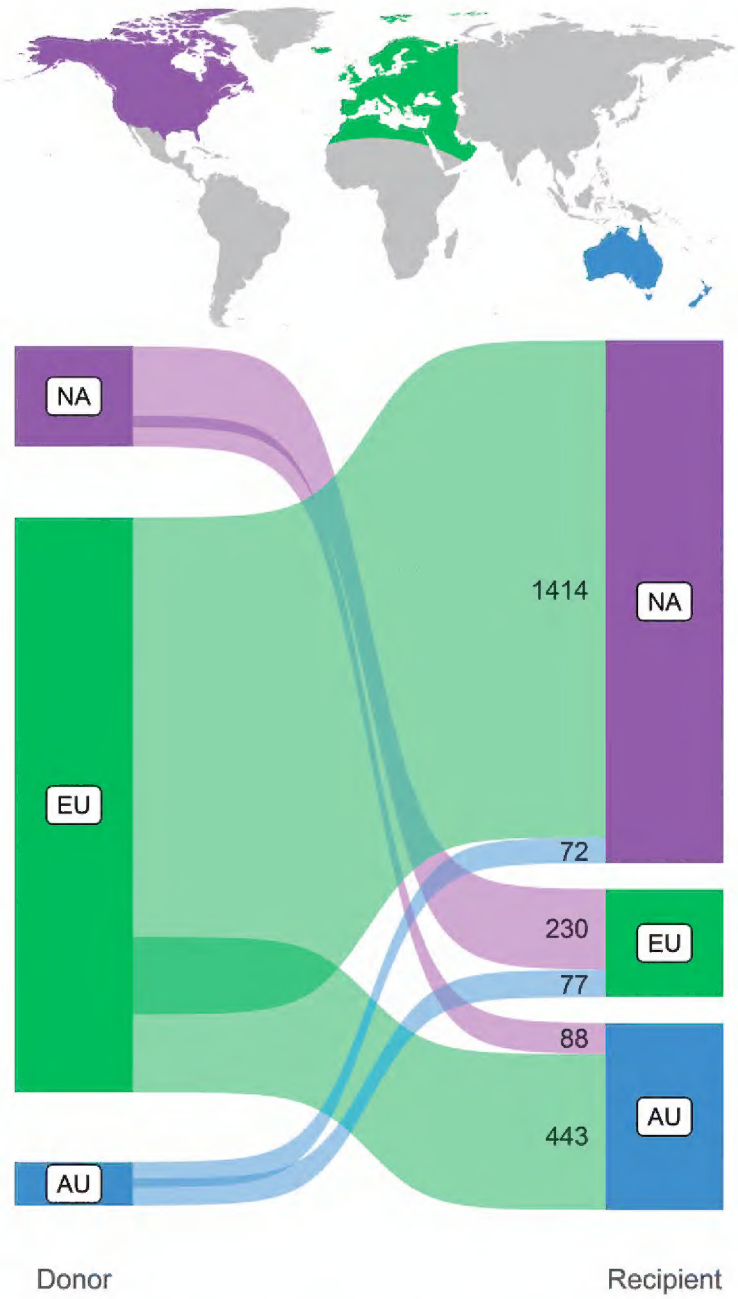

Figure 1. Flows of non-native insects between North America (NA), Europe (EU), and Australasia (AU). Numbers indicate the total count of species established from donor to recipient, with flow widths being proportional to these counts. Overlapping flows on the donor side indicate the fraction of species that established in both recipient regions.

many cases (Europe to North America and Australasia, and North America to Australasia), the rates of establishment of non-native insects per billion pounds sterling (hereafter referred to simply as establishment rates) were greatest near the very start of the dataset (circa 1827). These rates decreased over time, particularly between 1940 and 1960, with our models explaining these declines as depletion of the invader pools. Approximately 75% of non-native insect species that established from Europe into North America and Australasia had done so by 1950 (Fig. 2a, c). In contrast, the establishment rates of North American insects into Europe have decreased only very slightly over time (Fig. 2b), and there is no evidence (as per AIC-based model selection) of any decline in the establishment rates of Australasian insects into Europe (Fig. 2d, Table 2).

Discoveries and modelled establishments of non-native insects between North America and Australasia were within the same order of magnitude in both directions

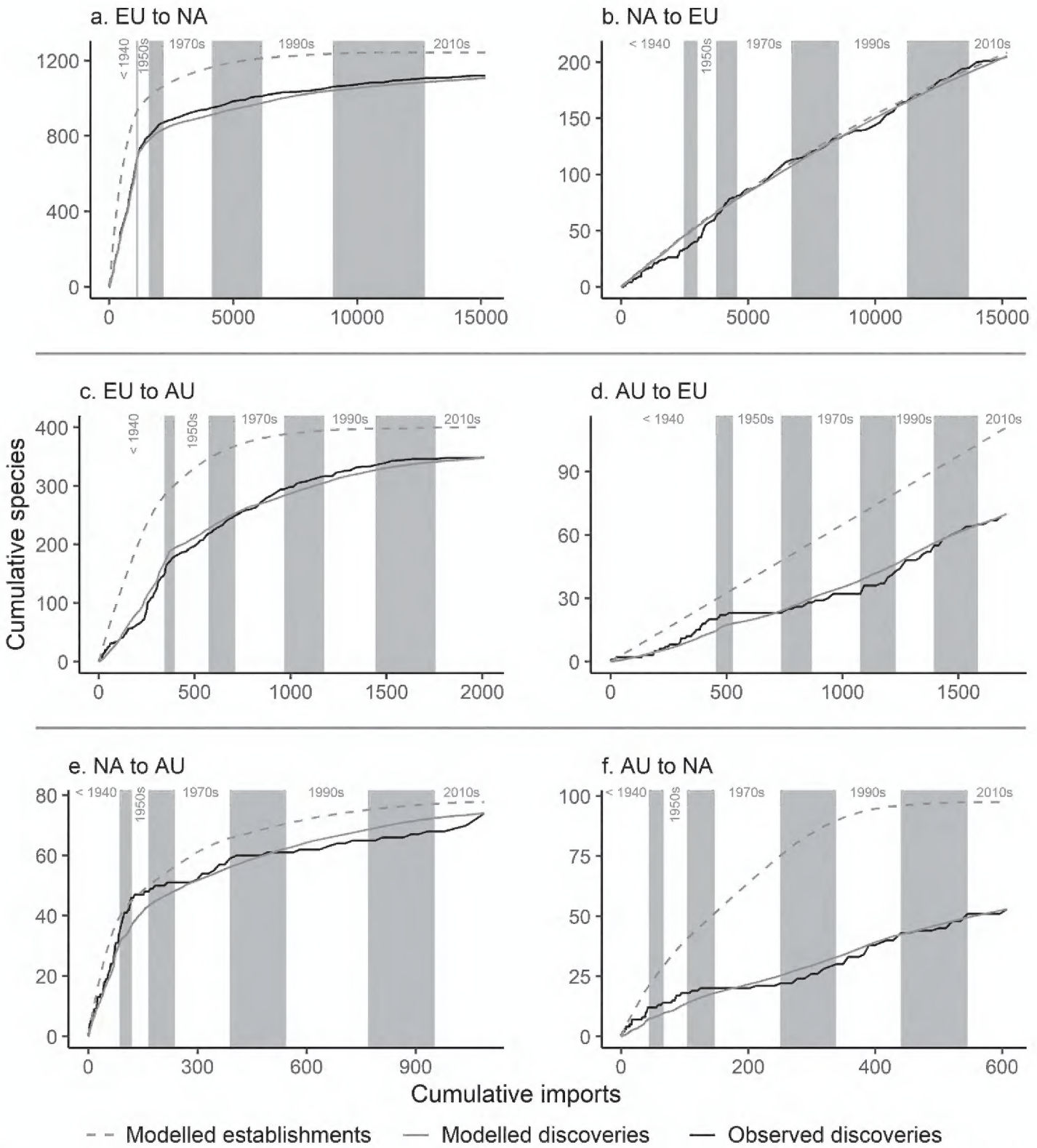

Figure 2. Cumulative discoveries (observed and modelled) and establishments (modelled) of non-native insects exchanged between Europe (EU), North America (NA), and Australasia (AU) versus cumulative import value (inflation-corrected to 2020 British pounds sterling, billions), 1827–2014. Alternating background shading indicates decadal increments, with shading omitted prior to the 1940s for clarity.

(Fig. 2e, f). There was evidence of saturation in the flows of non-native insects between North America and Australasia, though less so from Australasia to North America.

The modelled numbers of non-native insect establishments per billion pounds sterling (annual establishment rate, r) were significantly different for the reciprocal flows between Europe and North America and between Europe to Australasia (Table 2). Between Europe and North America, the predicted sizes of the invader pools (based on the number of discoveries at maximum establishments, d_{sat}) favors Europe, but with overlapping 95% confidence intervals (Table 2).

Table 2. Parameters and 95% confidence intervals of Poisson-process models of establishments and lagged discoveries of non-native insect species exchanged between Europe (EU), North America (NA), and Australasia (AU). All models included a parameter for imports (r, the number of annual establishments per billion pounds sterling) and lag (π, the annual probability of discovery of established species). Models including an additional term for saturation (a decrease in establishment probability as the cumulative number of discoveries approaches d_{sat}) were selected in most cases, with model selection based on Akaike information criterion (AIC) values.

Flow	Best model (ΔAIC of next-best model)	Annual establishment rate, r (95% CI)	Discoveries at maximum establishments, d_{sat} (95% CI)	Annual discovery probability, π (95% CI)	Lag years (95% CI)
EU to NA	Imports + saturation + lag (2118)	1.58 (1.40–1.77)	1121 (1089–1153)	0.0277 (0.0345–0.0208)	36.1 (29.0–48.0)
NA to EU	Imports + saturation + lag (6.08)	0.0194 (0.0144–0.0245)	701 (290–1114)	0.499 (1–0)	2.0 (1.00–∞)
EU to AU	Imports + saturation + lag (251)	1.212 (0.825–1.60)	366 (312–419)	0.0245 (0.0386–0.0103)	40.9 (25.9–96.7)
AU to EU	Imports + lag (2.0*)	0.0647 (0.0173–0.112)	n/a	0.0259 (0.0690–0)	38.5 (14.5–∞)
NA to AU	Imports + saturation + lag (99.6)	0.771 (0.448–1.09)	76 (68–83)	0.0721 (0.141–0.00354)	13.9 (7.11–283)
AU to NA	Imports + saturation + lag (8.37)	0.621 (0–2.23)	53 (1.60–104)	0.0153 (0.0598–0)	65.5 (16.7–∞)

* Although this low ΔAIC could be considered "substantial evidence" for both the full and reduced model (Burnham and Anderson 2004), the d_{sat} parameter estimate in the full model greatly exceeded the number of insect species in the donor region, thus the full model effectively lacked saturation and was not ecologically appropriate.

Discussion

Considerably more insect species have invaded North America and Australasia from Europe than in the opposite directions. This concurs with the previously observed overrepresentation of tree-feeding insects from Europe in North America (Niemelä and Mattson 1996), and with non-native insects from the western Palearctic (i.e., Europe) being overrepresented in New Zealand (Edney-Browne et al. 2018). Our results demonstrate that these asymmetries are consistent across all insect orders considered in the analysis, including both herbivorous and non-herbivorous insects.

International trade is considered the single most important pathway for unintentional introductions of insects (Brockerhoff and Liebhold 2017), and greater trade activity generally results in greater propagule pressure of non-native species. Existing literature identifies a positive correlation between import value and the establishment of non-native species (Levine and D'Antonio 2003; Seebens et al. 2017; Lantschner et al. 2020; MacLachlan et al. 2021). Similarly, our models provided excellent fits of inflation-corrected import values to temporal changes in non-native insect establishment rates (after accounting for gradual depletion of source pools). However, the modelled establishment rates (r), which represent the maximum rates of establishments per billion pounds sterling of imports prior to any depletion of source pools, differed significantly between the Europe to North America flow and its converse, and between the Europe to Australasia flow and its converse (Table 2). These significant differences

indicate that even after accounting for differences in trade values, large asymmetries between flows remain unexplained by the models. Contrary to our expectations, and despite the important role of trade in facilitating the establishment of non-native species, we must look to other explanations for these asymmetries.

Temporal variation in establishment rates may hold some clues as to the possible causes of the invasional asymmetries. While global establishments of non-native species have not slowed (Seebens et al. 2017; MacLachlan et al. 2021), our results show that establishment rates may be slowing down at regional scales. Establishments of European insects in North America and Australasia per billion pounds sterling of imports have drastically decreased since 1950 (Fig. 2a, c). Several authors have noted or predicted similar declines in the rate of accumulation of exotic species into the United States (Levine and D'Antonio 2003; Liebhold et al. 2017; MacLachlan et al. 2021; Seebens et al. 2021), with two possible explanations offered: depletion of source invader pools, or improved biosecurity measures.

Unequal flows of non-native insects may arise from differences in the numbers of potential invaders present in the donor regions (Vermeij 1991). Our models attempted to predict the size of these invader pools, provided that a decreasing trend in establishment rates could be suitably explained (based on ΔAIC) by the depletion of these pools. Our results suggest that some of the asymmetry in non-native insects exchanged between Europe and North America may be due to a ~60% larger pool of European insect invaders. However, this was not a significant difference, given the large confidence intervals around these estimates. Described insect species richness in Europe is approximately equal to that of North America (de Jong et al. 2014; Arnett 2000). Again, this suggests that the asymmetry between Europe and North America cannot be explained by differences in invader source pool sizes (assuming that the ratio of described to undescribed species is not strikingly greater in North America and Australasia than it is in Europe).

Scientific effort almost certainly varies regionally, and this may impact the interpretation of our results. Over the last few hundred years, Europe has had a consistently greater population density than either North America or Australasia (Goldewijk 2005). If this corresponds to greater scientific effort in Europe (more biologists/naturalists per unit area), the proportion of established species which have been discovered and the proportion of native species which have been described are likely greater in Europe than in North America and Australasia. This has several implications for our analyses. First, it suggests that we may have relatively underestimated the numbers of European insects in North America and Europe and thus the asymmetries may be even more dramatic than our analyses suggest. Second, the published counts of described insect species may be biased in favor of a relatively greater number in Europe, which may predispose us towards suggesting that the asymmetries are due to a greater richness of European invaders. We attempted to account for differential scientific effort in our models, in the form of an annual probability of detection that could vary independently for each of the six flows. Unfortunately, this parameter seldom had a clear optimum, and the resulting confidence intervals are large. These wide confidence intervals may be due in part to using a fixed annual probability of detection (unchanging over

time). Future research may benefit from allowing the discovery probability to change over time, perhaps by incorporating regional time series of proxies for scientific effort.

Despite the lack of statistical significance, the larger estimate for the pool of European insect invaders in North America versus the opposite could be considered a point in favor of the European crucible hypothesis proposed by Niemelä and Mattson (1996). This hypothesis suggests that a history of extensive glaciations may have reduced the niche diversity and 'invasibility' of Europe by leading to extinctions of plant genera, while simultaneously selecting for competition-hardened species that thrive in disturbed habitats, making European species better invaders. However, Europe has been heavily colonized by insects from regions other than North America, particularly the Asian Palearctic (Roques et al. 2020), suggesting that Europe is not notably resistant to invasion. Additionally, our models suggest that European insects established into North America 81 times more quickly (per billion pounds sterling of imports) than North American insects established into Europe. If this remarkable difference could be explained largely by European insects being better invaders, we would expect model estimates of the invader pool sizes between Europe and North America (using d_{sat} as a proxy) to be considerably more different than they were found to be, and significantly so.

Although we have modelled declining establishment rates as the gradual depletion of source invader pools, it is also likely that biosecurity measures have contributed. International biosecurity regulations, specifically phytosanitary measures, began in earnest in the 20th century (Roques 2010; Allen et al. 2017). With plant-feeding insects making up 58% of all non-native insect species in our dataset, strengthened phytosanitary measures applied to pathways including live plants, wood, and crops have almost certainly led to contemporary reductions in establishment rates. Europe has also had less strict phytosanitary measures than Australia and New Zealand for many decades (Eschen et al. 2015), which may partly explain the relative lack of declines in the rates of discoveries of North American and Australasia insects (per billion pounds sterling) in Europe. However, strengthening biosecurity efforts are most likely to have influenced the latter half of our time series (1900 and onwards), whereas considerable asymmetry in the numbers of species exchanged between Europe, North America, and Australasia had already accumulated by 1900. Therefore, differential biosecurity is an unlikely driver of these asymmetries.

Though historical invasion discoveries began much earlier, available import data only began in 1827. Given that the greatest establishment rates were seen at the very start of the dataset, it is possible – perhaps even likely – that the main causal agents explaining the dominance of Europe as a source of non-native insects in North America and Australasia were transient phenomena that began prior to 1827. This is complicated further by invasion biology being a relatively new discipline: early records of novel species may be both lacking and underrepresented in scientific literature. After a non-native species establishes, there is typically a time lag until it is discovered (Essl et al. 2011). Although our models attempt to account for lags between establishment and discovery, we used an annual probability of detection that does not change over time, and the lag estimates often have wide confidence intervals. Therefore, we are not confident that our data could be used to extrapolate far into the past.

Well before our dataset begins, North America and Australasia were experiencing a period of dramatic change as European colonies were founded. This colonization promoted both deliberate and accidental introductions of European plants (Lenzner et al. 2018). Introductions of exotic plants by colonial powers accelerated in the 19th and early 20th centuries, with a lasting impact on the global composition of floral communities (Lenzner et al. 2022). This is noteworthy, because plant imports and introductions may be a strong predictor of insect invasions (Liebhold et al. 2012; Liebhold et al. 2018; Bonnamour et al. 2023). North America and Australasia each have nearly twice as many extra-continental non-native plant species as Europe, and Europe is second to Asia as a dominant source of non-native plants worldwide (van Kleunen et al. 2015). This history, and the close relationships between insects and plants, suggest a potential explanation for both the existence of the asymmetries we observe and their temporal trends. We suggest that future research focuses on European colonization and coincident plant introductions as possible explanations for why Europe has donated so many more non-native insects into North America and Australasia than it has received from these regions.

We cannot rule out other factors not addressed here, such as differences in establishment probability driven by climate suitability or biotic resistance, the effect of establishments originating from non-native populations ('bridgeheads'), or differences in propagule pressure driven by the specific types of trade goods exchanged between regions. This latter factor is likely the most important to consider for future research, as overall import values may not capture changes over time in the relative contribution of specific commodities (such as plants and plant products) to overall trade. From the discussion above, we know to expect close associations between insects and plant products. Plant products may also have low values per unit of volume, thus being poorly represented in overall import values. Analyses which considered different commodities separately were conducted by Morimoto et al. (2019) but these were limited to Japan, 1951–2016. Data for continent-scale regions (i.e., North America and Europe) going back into the early 1800s do not exist, so far as we are aware, in any cohesive form. To compile such data from historical records would be a major interdisciplinary effort and was beyond the scope of our present research. Regardless, our results are an important step forward in confirming the existence of strong asymmetries in insect establishments between our focal regions and suggesting possible explanations for their cause.

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Supplementary material 1

Data for Asymmetrical insect invasions between three world regions

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Data type: docx

Explanation note: Annual (1827–2014) and undated discoveries of non-native insects and annual inflation-corrected import values (in 2020 British pounds sterling, billions) exchanged between Europe (EU), North America (NA, north of Mexico) and Australasia (AU, Australia and New Zealand only).

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